NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVIII(2), 1980, pp. 133–142

ANATOMY OF THE MALE REPRODUCTIVE SYSTEMS OF THE ADULTS AND PUPAE OF TWO DORYLINE ANTS, *DORYLUS* (*ANOMMA*) *WILVERTHI* EMERY AND *D.* (*A.*) *NIGRICANS* ILLIGER[1,2]

Francis C. Ford[3] and James Forbes

Abstract.—This is the first study of the anatomy of the male reproductive systems of the adults and pupae of the doryline ants, *Dorylus* (*Anomma*) *wilverthi* and *D.* (*A.*) *nigricans* Illiger. The external genitalia and the terminal gastric sterna are included. The reproductive systems consist of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia. The external genitalia of these ants are composed of a basal ring and three pairs of valves, the outer, the middle, and the inner, typical of the formicid pattern. The male systems in these two species are similar in their shapes and the arrangement of the organs. Although the testes in the *nigricans* adult are absent, in the pupa there are 50–55 follicles in each testis. *Wilverthi* has 35–40 testicular follicles in both the adult and pupa. The valves of the external genitalia and terminal gastric sterna of these two species show no individual variations, other than size, in their shapes. Male systems have been described for only three other doryline ants, the Old World *Dorylus labiatus,* the New World *Eciton hamatum* and *Neivamyrmex harrisi.* This system is compared in these dorylines. Important differences exist between the male reproductive systems of the two African *Dorylus* species herein studied and the two New World dorylines previously reported. The *Dorylus* species have a larger number of testicular follicles, the shapes of their accessory glands are different, the basal ring of the genitalia is fused to the outer valves, a membrane joins the ventral margins of the inner genitalic valves, and the shapes of the genitalic valves and the subgenital plate are different.

This paper presents the first description of the anatomy of the male reproductive systems of the adults and pupae of two Old World dorylines, *Dorylus* (*Anomma*) *wilverthi* Emery and *Dorylus* (*Anomma*) *nigricans* Il-

---

[1] Hymenoptera: Formicidae.

[2] Part of the Ph.D. dissertation of the first author at the Department of Biological Sciences, Fordham University.

[3] Present address: Department of Biology, Bronx Community College, CUNY, Bronx, N.Y. 10453.

liger. Descriptions of the genitalic valves and the terminal gastric sterna are also included. Male systems have been described for only three other dorylline ants, the Old World *Dorylus labiatus* (Mukerjee 1926), the New World *Eciton hamatum* (Forbes 1958) and *Neivamyrmex harrisi* (Forbes and Do-Van Quy 1965). This system will be compared in these dorylines.

Seven to nine specimens each of the adults and the pupae were kindly furnished by Albert Raignier, S.J. of Belgium, who collected these ants in the Republic of the Congo, Africa, now designated Zaire, during June of 1956 and November of 1957. The pupae were advanced in development. The entire reproductive systems were dissected from the gasters of the adults and pupae, stained with borax carmine, and prepared as whole mounts for study. The external genitalia and terminal segments were also removed and mounted for study. Illustrations were prepared with the aid of a B and L trisimplex microprojector.

The reproductive systems consist of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia (Figs. 1–3). Throughout the following descriptions, the adult system of *wilverthi* will be described first, followed by differences in the pupal system. Comparisons will then be made with the adult and pupa of *nigricans*.

The testes of *wilverthi* are located in the dorsal median region of the gaster and extend through the 2nd and 3rd gastric segments above the ventriculus (Fig. 1). The posterior portion of each testis overlies most of the seminal vesicles. Each testis is composed of about 35–40 slender, thin-walled testicular tubules that are about 8 mm in length. Each tubule ends in a narrow duct, a vas efferens. The number and the arrangement of the testicular tubules in the pupa of *wilverthi* are similar to those of the adult. In the adult of *nigricans* the testes and vasa efferentia are absent. However, in the pupa each testis consists of 50–55 tubules, and it is similar in its shape and position to that of *wilverthi*. The testes of these two species are not covered with connective tissue sheaths or capsules.

The vasa efferentia join to form a short duct, the vas deferens. Where the vasa efferentia unite, the vas deferens is slightly more dilated than it is distally. The distal portion enters the expanded seminal vesicle just below its anterior end. The vas deferens is absent in the adult of *nigricans* but present in the pupae of *wilverthi* and *nigricans*.

The seminal vesicles are large, prominent, thick-walled, U-shaped tubes that lie in the 3rd and 4th gastric segments (Fig. 1). The first part of the proximal arm lies at right angles to the direction of the testicular tubules. It continues forward and ventrolaterally, then bends sharply posteromediad toward the posterior region of the ventriculus. The proximal arm is slightly shorter than the distal, but both arms are nearly equal in diameter. The

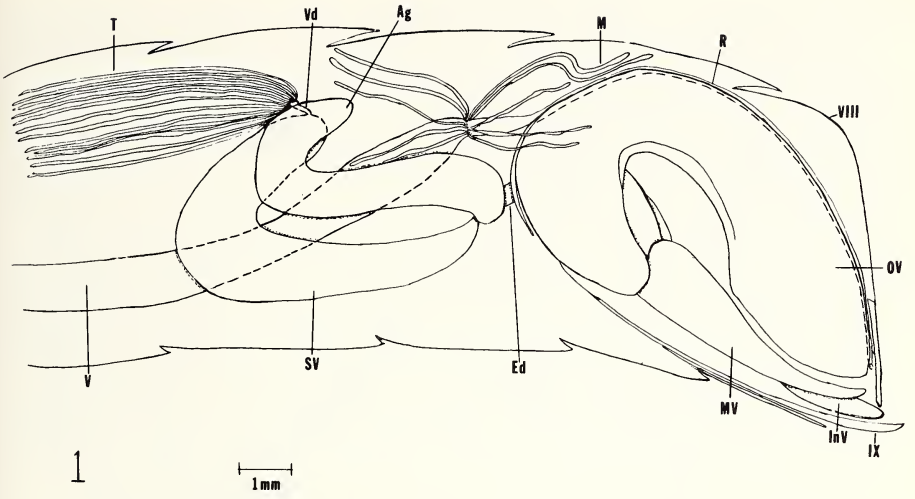
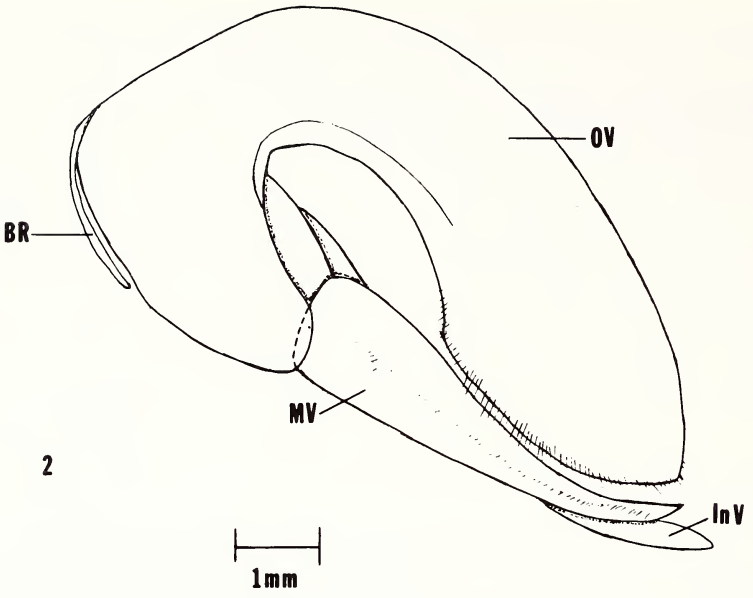


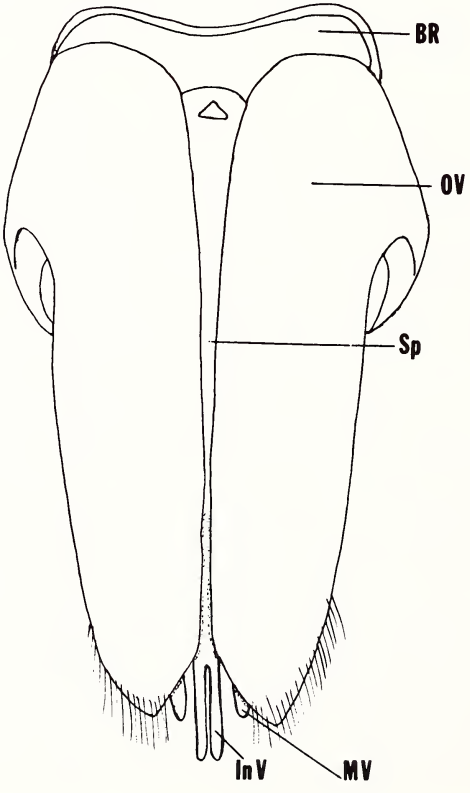
Fig. 1. Diagram of a lateral dissection of the posterior portion of the gaster of the adult male ant *Dorylus* (*Anomma*) *wilverthi*. Abbreviations: Ag, accessory gland; Ed, ejaculatory duct; InV, inner valve; M, Malpighian tubule; MV, middle valve; OV, outer valve; R, rectum; SV, seminal vesicle; T, testis; V, ventriculus; Vd, vas deferens; VIII–IX, Roman numerals designate abdominal segments.

position and arrangement of the seminal vesicles in the pupa of *wilverthi* and in the adult and pupa of *nigricans* are similar to that in the adult of *wilverthi*. Differences in the diameters of these organs between the adults of *wilverthi,* the larger species, and *nigricans* are about 25–30 percent. Likewise in both species, the diameters of the seminal vesicles of the pupae are about ¼ to ⅓ smaller than those of the adults. The seminal vesicles of the *nigricans* adults were packed with sperm, while those of *wilverthi* had sperm scattered throughout. No sperm is present in these organs in the pupae. Toward the posterior margin of the 4th gastric segment each seminal vesicle tapers gradually, bends dorsomedially, and joins the accessory gland on its ventromedian surface.

Each accessory gland is a prominent, thick-walled, S-shaped tube lying above the seminal vesicles, and located on either side of the posterior region of the ventriculus (Fig. 1). Their free ends are close to the midline and point forward. The gland bends sharply laterally and anteriorly a short distance, then dips ventroposteriorly, turns toward the midline at the posterior margin of the 4th gastric segment, where the seminal vesicle joins it on its ventromedian surface. Beyond this junction each accessory gland tapers slightly, joins the gland from the other side, and forms a single tube. The first portion of this tube is the bound accessory gland duct, and the end portion where



2



3

the wedge is located is the ejaculatory duct. The bound accessory gland duct bends dorsally at the anterior edge of the 5th gastric segment.

The ejaculatory duct passes through the basal ring and between the anterior borders of the large, prominent, outer genitalic valves and enters the middorsal surface of the aedeagal bladder (Figs. 1 and 4). The posterior end of the ejaculatory duct is depressed into the middorsal wall of the aedeagal bladder.

The aedeagal bladder is a muscular-walled, ovoid sac that lies beneath the basal portions of the inner genitalic valves, and it opens posteriorly between the inner valves. Muscle fibers on the outer wall of the aedeagal bladder are attached to the anteroventral surfaces of the inner valves.

The accessory glands, the bound accessory gland ducts, the ejaculatory ducts and the aedeagal bladders in the *wilverthi* pupa and the *nigricans* adult and pupa are similar to those of the *wilverthi* adult.

Genitalia and Terminal Gastric Segments

The external genitalia of *wilverthi* and *nigricans* (Figs. 1 through 6) are retracted into a cavity within the last few gastric segments beneath the rectum and the anus, and only the posterior tip of the ninth sternum or subgenital plate projects from the end of the gaster. This arrangement is characteristic of the dorylines (Borgmeier 1955). The external genitalia of these ants are composed of a basal ring and three pairs of valves, the outer, the middle, and the inner, typical of the formicid pattern (Clausen 1938; Snodgrass 1941; Krafchick 1959).

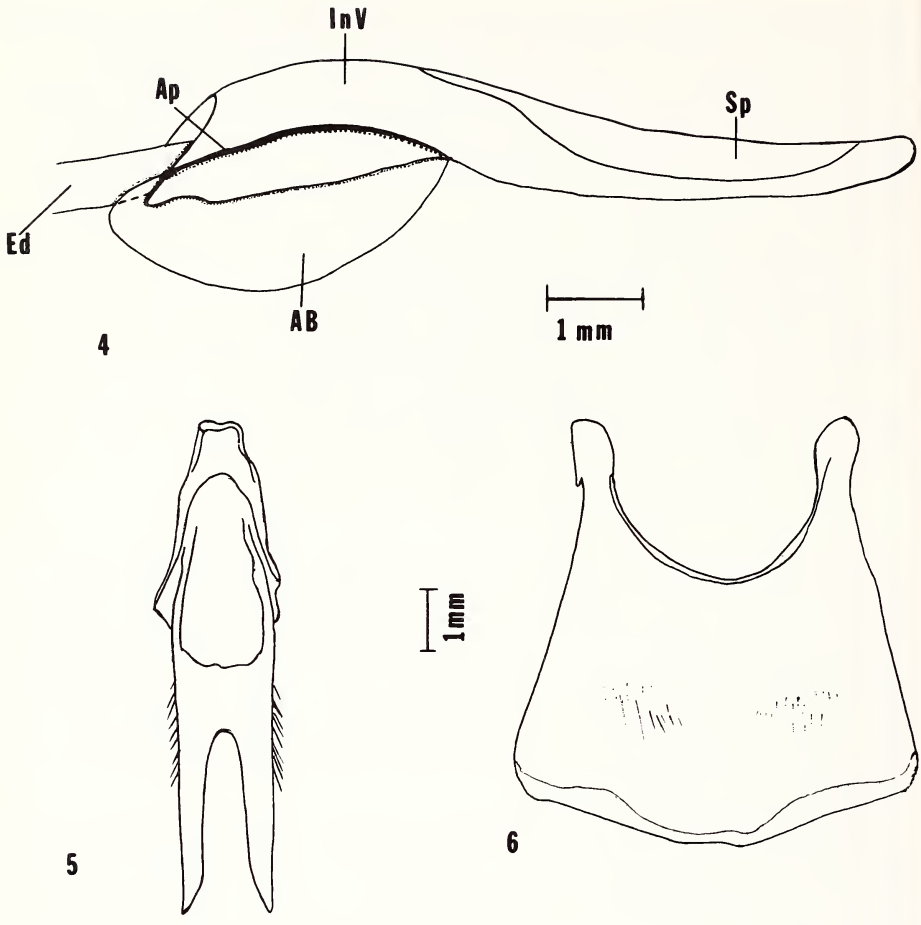
The basal ring or lamina annularis is a narrow, ring-like segment that is moderately sclerotized throughout (Figs. 2 and 3). The dorsal part is wider than the lateral and ventral portions, and it is fused to the dorsal, anterior borders of outer valves; its middorsal region forms a bridge between the outer valves. On the ventral part there is a small middorsal apodeme.

The outer valves or parameres are the largest and most heavily sclerotized of the three pairs (Figs. 2 and 3). They are laterally convex. From a side view the overall shape of the valve is somewhat C-shaped with the open part of the C directed downward. There is no division into an anterior lamina parameralis and a posterior paramere. The anterior portion of the valve is large and cup-shaped, and it covers the anterior tips of the middle valves and the bases of the inner valves. The posterior portion of the valve, when

---

←

Figs. 2, 3. 2. Diagram of a lateral view of the male genitalia of *wilverthi*. 3. Diagram of a dorsal view of the male genitalia of *D. wilverthi*. Both diagrams are drawn to the same scale. Abbreviations: BR, basal ring; InV, inner valve; MV, middle valve; OV, outer valve; Sp, spathe.



Figs. 4–6. 4. Diagram of a right lateral view of the ejaculatory duct, the inner genitalic valve, and the aedeagal bladder of the adult male of *D. wilverthi*. Abbreviations: AB, aedeagal bladder; Ap, lateral apodeme; Ed, ejaculatory duct; InV, inner valve; Sp, spathe. 5. Diagram of the dorsal view of the ninth sternum or subgenital plate of the male of *D. wilverthi*. 6. Diagram of a ventral view of the eighth sternum of the male of *D. wilverthi*.

viewed laterally enlarges slightly. The ventral margin of this posterior portion is covered with numerous, long, slender hairs. Dorsally and ventrally the outer valves are separated from each other.

The middle valves or volsellares are the shortest of the three pairs, and they are finger-shaped (Figs. 1, 2, and 3). The basal portion is the tallest, and it tapers posteriorly. The ventroanterior part of the basal portion is joined to the ventroposterior tip of the base of the outer valve by bands of muscle. These middle valves lie within the posterior portions of the outer

valves, and they extend as far as or slightly beyond the posterior margins of the outer valves. The outer surface of these middle valves is convex. Fine, sensory hairs extend along the middle of the outer surface of this valve.

The inner valves or laminae aedeagales constitute the aedeagus or male intromittant organ (Figs. 1 through 4). The basal portion of the valve is laterally convex and has a ridge-like apodeme on its outer surface. Numerous bands of muscle extend from the lateral apodemes to the inner surface of the base of the outer valves. The remaining two-thirds of these valves are bent downward in the middle, they are scimitar-like in shape, and they are heavily sclerotized except at their tips. A heavy, non-sclerotized membrane, the spathe, joins these valves dorsally almost to their tips. A small triangular sclerite is present on its anterior end. These valves are also united ventrally by a membrane that extends almost to their tips. These valves extend slightly beyond the posterior margin of the outer valves.

The eighth sternum is roughly rectangular in shape and moderately sclerotized throughout (Fig. 6). Its anterior border is thickened and deeply indented, while the posterior margin is weakly sclerotized and rounded in shape. Two patches of dark, sensory hairs are present on its ventral surface.

The ninth sternum, or subgenital plate, is narrow in shape, bifid posteriorly (Figs. 1 and 5), and is heavily sclerotized throughout. The anterior margin is thick; in the central region of this segment there is a depression on the dorsal surface into which many muscle fibers are inserted. Here, also, there are two small, lateral, triangular apodemes. The ventral surface of the posterior end is covered with many sensory hairs. Posteriorly the tips of the segment extend beyond the end of the gaster and the posterior margins of the external genitalia.

In the *wilverthi* pupa the arrangement, shapes, and position of the valves and terminal gastric sterna are similar to those of the adult, but they are not as heavily sclerotized; in the adult they are dark brown in color. In the *nigricans* adult and pupa the arrangements, shapes, and positions of the valves and terminal gastric sterna are similar to those of *wilverthi,* and these structures in the pupa are less sclerotized. The genitalic valves and the terminal gastric sterna in *nigricans* are smaller in size, it is a smaller ant, and they are reddish-yellow in color.

Discussion

The testes in the adults and pupae of *wilverthi* and the pupae of *nigricans* are large and extend through the second and third gastric segments. The testes in the adults of *nigricans* are absent. In *N. harrisi* (Forbes and Do-Van Quy 1965) the testes are small and lie in the posterior region of the third gastric segment, in *E. hamatum* (Forbes 1958) they are large and

extend through the first three gastric segments, and in *D. labiatus* (Mukerjee 1926) no specific location was designated. The testicular follicles in both *wilverthi* adults and pupae, and *nigricans* pupae are long, slender tubules, 35–40 in each testis of *wilverthi* and approximately 50–55 in each testis of *nigricans*. The testicular follicles in *N. harrisi* and *E. hamatum* are long, slender tubules, 22–25 in each testis of *N. harrisi* and 20 in each testis of *E. hamatum*. In *D. labiatus* each testis contains "a fair number" of tubular follicles. The testicular follicles of all of the ants end in short narrow ducts, the vasa efferentia.

No connective tissue sheath covers the testes of the two *Dorylus* species herein reported. A single capsule covers the testes in *N. harrisi,* while each testis is covered by a capsule in *E. hamatum*. No capsule is reported by Mukerjee (1926) in *D. labiatus*. In *wilverthi* and *nigricans* the vasa efferentia join to form a short duct, the vas deferens. This arrangement is similar in *N. harrisi* and *E. hamatum*. Structures comparable to vasa efferentia are shown, but not labelled, by Mukerjee in his illustrations of the reproductive system of *D. labiatus*.

The seminal vesicles in *wilverthi* and *nigricans* adults and pupae are prominent, thick-walled, U-shaped tubes lying in the third and first half of the fourth gastric segments. In *N. harrisi* (Forbes and Do-Van Quy 1965) and *E. hamatum* (Forbes 1958) the position, shape, and arrangement of these organs are similar to that in *wilverthi* and *nigricans*. The terminology of this organ in male ants has been clarified by Hung and Vinson (1975). Mukerjee (1926) reports an organ in *D. labiatus* that he calls the seminal duct and describes a swelling at the anterior end, the collecting sac, and a larger dilation at its posterior end, the vesicula seminalis. He reports that this organ is usually U-shaped and also notes variations in the position and size of the vesicula seminalis. In this study nothing resembling the description and diagram of the seminal duct of *D. labiatus* was found.

The accessory glands in the adults and pupae of *wilverthi* and *nigricans* are prominent, thick-walled, S-shaped tubes lying in the fourth gastric segment. In *N. harrisi* and *E. hamatum* the accessory glands are tightly coiled tubes situated on either side of the intestine in the fourth gastric segment. The accessory glands of *D. labiatus* are large, slightly curved, thick-walled tubes, which in some cases have an appendix. Mukerjee indicates variations and anomalies in the reproductive system of *D. labiatus*. No such anomalies or variations were observed in the small number of specimens available for this investigation.

The bound accessory gland duct in *wilverthi* and *nigricans* is very short. In *N. harrisi* this organ is approximately equal to the accessory gland in length. In *E. hamatum* this duct encircles the ventriculus five or six times and is 28 to 31 mm in length. In *D. labiatus* no bound accessory gland duct

is reported, although a portion of what is shown as the ejaculatory duct may be the bound accessory gland duct.

The ejaculatory duct in *wilverthi* and *nigricans* is similar to that of *N. harrisi* and *D. hamatum,* and in all these ants a cuticular wedge is present in this organ. The ejaculatory duct, illustrated by Mukerjee (1926) in *D. labiatus* appears to be long, and he shows a wedge-shaped structure in the posterior part of this duct which he designates "penes." He found in a single specimen a blind diverticulum on the dorsal side of this duct. No such structure has been reported in any other doryline.

An aedeagal bladder is present in *wilverthi,* and *nigricans* as well as *N. harrisi* and *E. hamatum.* Mukerjee (1926) made no mention of this organ in *D. labiatus.*

The valves of the external genitalia and the terminal gastric sterna of these two *Dorylus* species show no individual variations, other than size, in their shapes. This is contrary to what Borgmeier (1955) reported in his study of the Neotropical dorylines where even in what may be related species distinctive differences are present in some genitalic valves and the subgenitalic plate.

Important differences, therefore, exist between the male reproductive systems of the two African *Dorylus* species herein studied and the two New World dorylines previously reported. The *Dorylus* species have a larger number of testicular follicles, the shapes of their accessory glands are different, the basal ring of the genitalia is fused to the outer valves, a membrane joins the ventral margins of the inner genitalic valves, and the shapes of the genitalic valves and the subgenital plate are different.

Literature Cited

Borgmeier, G. 1955. Die Wanderameisen der Neotropischen Region (Hymenoptera, Formicidae). Studia Entomologia, Nr. 3, Editora Vozes Limitada, Petropolis, R. J. Brasil, 3:9–716.

Clausen, R. 1938. Untersuchungen über den männlichen Copulatinsapparat der Ameisen, speciell der Formicinae. Mitteil. Schweizer. Entomol. Gesells. 17:233–346.

Forbes, J. 1958. The male reproductive system of the army ant, *Eciton hamatum* Fabricius. Proc. Xth Internat. Congr. Entomol. 1:593–596.

——— and D. Do-Van-Quy. 1965. The anatomy and histology of the male reproductive system of the legionary ant, *Neivamyrmex harrisi* (Haldman) (Hymenoptera: Formicidae). J. N.Y. Entomol. Soc. 73:95–111.

Hung, S. C. F. and S. B. Vinson. 1975. Notes on the male reproductive system in ants (Hymenoptera, Formicidae). J. N.Y. Entomol. Soc. 83:192–197.

Krafchick, B. 1959. A comparative study of the male genitalia of North American Ants (Formicidae) with emphasis on generic differences. Dissertation, University of Maryland.

Mukerjee, D. 1926. The digestive and reproductive systems of the male ant, *Dorylus labiatus* Schuck. J. and Proc. Asiatic Soc. Bengal, n. s. 22:87–92.

Raignier, A. and J. Van Boven. 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma*. Ann. Mus. R. du Congo Belge, Sc. Zool. 2:1–359.
Snodgrass, R. 1941. The male genitalia of Hymenoptera. Smithson. Misc. Col. 99, No. 14. 86 pp., 33 pls.

Department of Biological Sciences, Fordham University, Bronx, New York 10458.

Received for publication December 17, 1979.